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# THE BOTANICAL GAZETTE

*October 1922*

## HETEROTHECA GRIEVII THE MICROSPORANGE OF HETERANGIUM GRIEVII

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(WITH PLATES IV, V, AND EIGHT FIGURES)

### Introduction

The sporangia here described have so far only been recorded from the Pettycur deposits of the Calciferous Sandstone Series of Scotland. They have been found in three blocks, one of which, presented to the writer by Professor BAYLEY BALFOUR in 1905, yielded also some of the specimens of *Sphaerostoma* of which a description has already been published (5); the other two blocks were collected at Pettycur by the writer in 1910. In all three blocks they were found associated with *Heterangium Grievii*. Their somewhat flattened fusiform shape is approximately that of *Telangium Scottii* (4), but the dimensions are less. *T. Scottii* measures about  $2 \times 3$  mm. in width at its maximum girth and 4 mm. in length, whereas the new sporange only measures roughly  $1 \times 2$  mm. in width and 3.5–4 mm. in length. A further resemblance to *Telangium* is their possession of longitudinal loculi or series of loculi, and of peripherally placed tracheids. These resemblances do not seem adequate to suggest its inclusion in this form genus, because there are many remarkably distinctive characters in the new form.

In the first place, each peripheral loculus of *Telangium* is represented in *Heterotheca* by a series of relatively small loculi.

Secondly, central loculi as well as peripheral ones occur in the new form. A third outstanding difference is the absence of any evidence that the sporangium underwent apical dehiscence, which is almost universally the case in species of *Telangium*, whether Lower Carboniferous (for example, *T. affine*) or Upper Carboniferous (for example, *T. Scottii*, etc.). The only exception known to me is a species<sup>1</sup> described by NATHORST (11). A fourth outstanding difference from *Telangium Scottii* (the only species so far described with structure preserved) is the presence in the new form of water storage tracheids, which, although few in the normal specimens, are very abundant in the partially sterile specimens. Lastly, a character is found which at first sight seems of minor importance. The new sporangium retains the twofold cortical sclerotic plates which form so characteristic a feature of the cortex of *Heterangium* stem and petiole. It is this latter feature which the writer regards as irrefutable evidence of the safe attribution of these microsporangia to *Heterangium Grievii*, with which they have invariably been found associated. Although, therefore, the sporangium has the same claim to the name of the parent plant as either stem or petiole, it has been found convenient to refer to it under the name of **Heterotheca Grievii**.

DIAGNOSIS.—I have founded the form genus *Heterotheca* for the reception of such microsporangia as resemble *Telangium* in form and possibly in insertion, but possess vertical sclerotic plates in their periphery and horizontal sclerotic plates deeper down in the cortex, like the vegetative organs of *Heterangium Grievii*. The loculi are not confined to the periphery, but central ones also occur.

The specific name of the form now described is that of the parent plant.

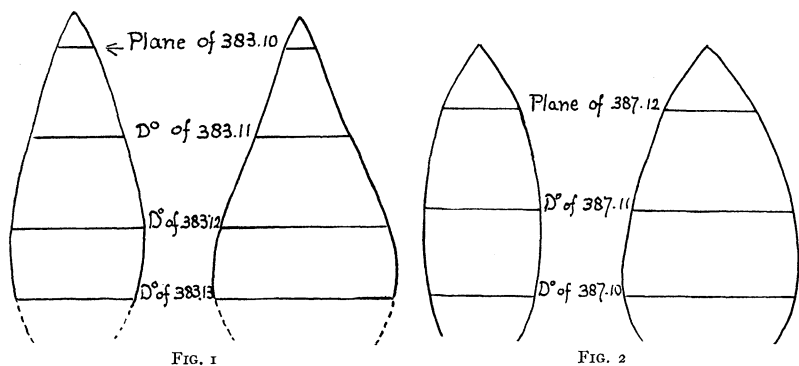
### Form, anatomical structure, and grouping of specimens

FORM.—The form of the sporangium can be deduced from the various series of sections through single specimens. Some of these have been plotted out to scale in text figs. 1 and 2. These show

<sup>1</sup> This species, of which the type specimen was figured by ARBER (1) under the name of *Carpolithus Nathorstii*, may prove to be a species of *Telangium*, owing to NATHORST'S discovery of its longitudinal loculi filled with microspores. The plate referred to exhibits what was possibly approximately the habit of *Heterotheca Grievii*.

*H. Grievii* to have had a tapering apex and a maximum girth nearer the base than the apex. The majority of the transverse sections through the upper part are circular, but in the basal region the sectional area is oval (figs. 8, 9), hence there are two aspects of each sporange given in text figs. 1 and 2.

In longitudinal sections the apical part is seen in surface view if present, as indicated in text fig. 3. In the upper third, the surface loculi are only slightly rubbed down in the center, the lateral ones being seen almost in surface view. If two sections are secured



FIGS. 1, 2.—Showing slightly bifacial form of sporange as indicated by plotting series of transverse sections to scale on vertical line; fifth section in series (CN. 383.14) just included five separated bases of loculi series, a fact on which the length (4 mm.) is deduced.

longitudinally through a single sporange, they are both somewhat peripheral, as the size of the body scarcely admits of two longitudinal sections. Both transverse series and longitudinal sections show that the sporange was almost always somewhat injured at the base where it has become detached from the parent plant.

ANATOMY.—The whole sporange is surrounded by a large-celled epidermis. The contents of the epidermal cells are carbonized, and from the mode of preservation of mucilaginous tissue in the Pettycur deposits, this blackened condition of the epidermis evidently precludes the view that it was mucilaginous (fig. 1). Beneath the epidermis is the hypoderm, composed of about five layers of cells. This tissue is continuous with the interstitial tissue between the loculi. In this cortical region are frequently found,

alternating with the peripheral loculi, especially near the apex and base, the characteristic vertical sclerotic plates of *Heterangium Grievii* (figs. 3, 4, 9, 13).

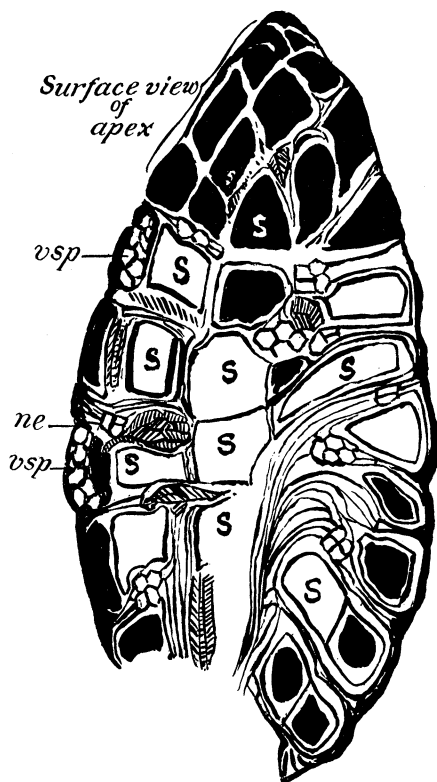


FIG. 3.—Diagrammatic drawing from two slightly oblique longitudinal sections (CN.386.17, 18), latter of which is nearly radial at base, and former superficial for upper third; it illustrates the somewhat spiral direction of locular series, preservation of spores in some but not in all loculi, vertical *Heterangium* sclerotic plates on left, large amount of water storage tissue and connecting tubules which abut on plates as in cortex of *Heterangium* petioles; sections were selected because of presence of ripe spores; central region is injured.

LOCULI.—The peripheral series of loculi which run longitudinally and somewhat spirally are more numerous than the loculi of *Telangium Scottii*, numbering in the middle zone of the sporangium twelve (figs. 3, 9; cf. also text fig. 4). Their approximation into groups is sometimes seen near the apex (CN.383.10). Immersed in the ground tissue of the central region of the sporangium, except at the extreme apex, there are further loculi, of which at least four appear in transverse sections (figs. 3, 12). Text fig. 3 is drawn from longitudinal sections too near the periphery to give the number and disposition of central loculi. The origin of additional central loculi by segmentation of peripheral loculi is suggested in some cases (text fig. 4), and the presence of ripe spores almost uniformly distributed in figs. 11 and 12 (CN.307.17, 18) suggests that the main content of the

young normal sporangium was potential sporogenous tissue. Each loculus is surrounded by a sheath of small, longitudinally ex-

tended, narrow cells. These sheaths, probably as a result of the shrinkage of the tissues due to carbonization, often become separated from the tissues which must have abutted on them in the living state. In the case of the central loculi the sheaths are often ruptured or entirely dissolved away, leaving the spores among the elements of the ground tissue (figs. 5, 11, 12). Small sclerotic plates often become incorporated with the walls of loculi, and when seen in profile are very characteristic (text figs. 4, 6,  $s^1p^1$ ).

In one synangium (figs. 11, 12) every loculus contains numerous ripe spores of tetrahedral form, similar in size and character to those in the pollen chamber of *Sphaerostoma ovale* (CN. 270.1) among specimens of which it lies (text fig. 5). The spores measure  $29\mu$  in their transverse and  $20\mu$  in their radial extent.

In this specimen some of the locular walls have broken down, but many of the peripheral and at least two of the central loculi are still intact. In other cases spores can be demonstrated only in some of the loculi, while others show opaque black or dark brown

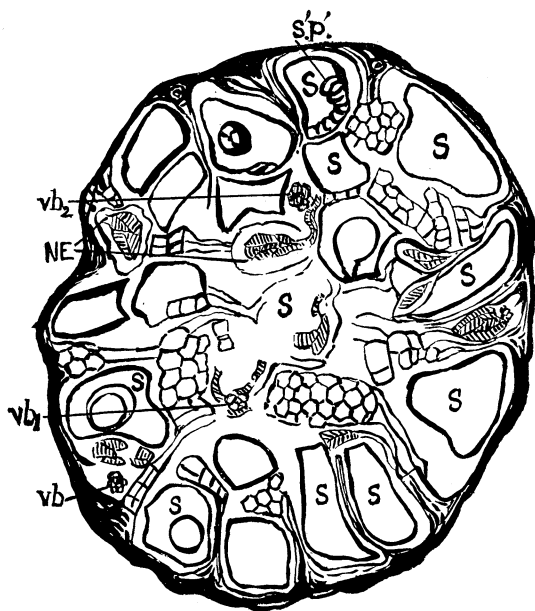


FIG. 4.—Diagrammatic drawing of transverse section of class II synangium (CN. 411.31); swollen ground tissue not entered in detail; two deeply lying vascular bundles shown in transverse section ( $vb_1$ ,  $vb_2$ ); one peripheral vascular bundle also cut transversely on left, but most are cut so obliquely that they are merely indicated by hatching; nerve ending seen near center with its delicate branch strand; one or two central loculi are broken down, and carbonization of peripheral ones probably explains absence of spores in some (cf. fig. 5); at  $s^1p^1$  a plate occurs attached to a loculus wall and is seen in profile as in CN. 307.18, for which consult text fig. 6 and fig. 12.

contents, a condition which is possibly the result of the conditions to which the sporangium was exposed during fossilization. As a rule the spores are better preserved in the interior than near the



FIG. 5.—Camera drawings of spores from loculi in CN.386.18 and CN.307.17; tetrad in middle is characteristic and possibly indicates residuum of spore mother still persisted as in recent cycads; spores on left drawn from those in pollen chamber of *Sphaerostoma* for comparison (CN.270.1).

surface, which may be due to the conditions of exposure being slightly different. In a large number of cases the contents of the loculi have entirely been dissolved, or are in an abnormal condition. Such are the series CN.383.10-13 and CN.386.11-12 (figs. 1-4).

In the series CN.391.23-27, slide 391.26 shows in two cases a nerve ending in the center of the abortive loculus. In a large number of cases the peripheral loculi have been carbonized, but not the central ones.

Swollen nerve endings accompanied by the *Heterangium* sclerotic plates appear to occupy the whole of the core of the sporangium in the most advanced phyllodic specimens (text fig. 7). I refer to the partially or entirely abortive specimens

as "phyllodic," as their tissues approximate the tissue elements of the ordinary sterile petiole of *Heterangium*. Moreover, they are linked together as in the petiole. There is a considerable range of form and size in the plates; some sporangia even seem to have produced more plates than others (fig. 12).

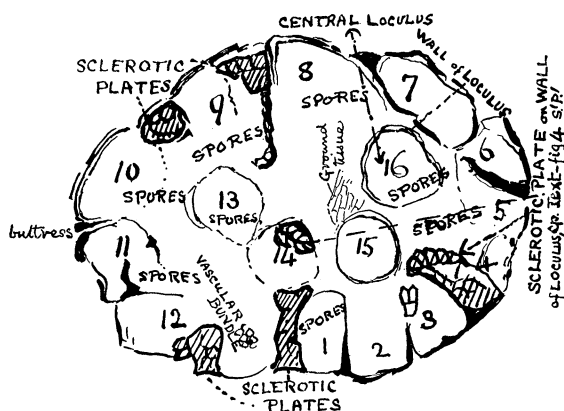


FIG. 6.—Key to fig. 12, showing outline of sclerotic plates, etc., which are clearer in slide than in micrograph.

The vertical plates in the periphery often have their cells thickened with layers of cell wall substance which almost obliterate the lumen of the cell; other plates are small, but most show the hexagonal form of cell indicated in text figs. 3 and 4. Abutting on these are tubular cells which are disposed mainly in the horizontal or transverse plane (text fig. 3). In the fossil these are generally swollen, and owing to their form and pale color have somewhat the appearance of macaroni. Some fibers accompany the delicate branches of the vascular bundles, and are continuous with a parenchymatous hood-like envelope to the nerve ending. Many, perhaps more in some specimens than in others, show a spiral line of thickening which resists imbibition and consequent swelling.

The six to eight mesarch strands of primary xylem which travel mainly in the peripheral region give off the delicate centropiscopically directed xylem strands, which end in the aqueous storage tissue. The contrast between the short barrel-shaped tracheids of the nerve ending and the slender carriers of the water is quite reminiscent of highly organized water storage organs in recent plants. The majority of the nerve endings in the synangium were directed to its central region. Transfusion elements of varying degrees of specialization are exceedingly abundant in some speci-

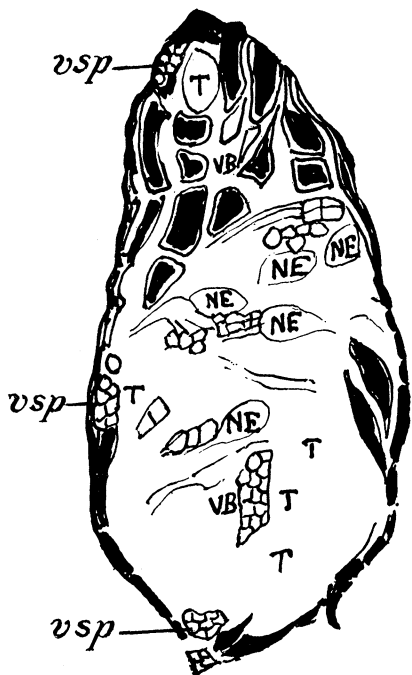


FIG. 7.—Camera sketch of specimen of *Heterotheca* in CN. 288.2; no carbonaceous matter is retained in center, and therefore lignified elements of ground tissue appear exceptionally clearly; five nerve endings, many transfusion elements, and two vascular bundles can be distinguished in original; distribution of vertical plates (*vsp*) characteristic; striated elements seen near apex as in many cases (cf. text fig. 3).



mens, and in some phyllodic specimens, such as that outlined in text fig. 7, where the carbonaceous matter is dissolved away in the center, the wide extent of the striated, possibly lignified, trans-fusion elements of the nerve endings is very clearly seen by the aid of the microscope. The nerve endings appear here to have wholly usurped the position of the central loculi (cf. fig. 6). The enlarged nerve ending is a familiar feature of the sterile pinna of *Lyginopteris*, and probably occurred in that of *Heterangium* also. The macerated condition of some of the specimens may be explained by the conditions to which they were subjected during fossilization. If we accept GORDON's explanation (8) of the mode of formation of the Pettycur plant deposits, we may attribute it partially to the action of thermal springs and warm pools in which the accumulation of the plant remains were deposited and gradually infiltrated.

Text figs. 3 and 4, which illustrate the preceding statements, are both mere diagrams based on definite sections showing ripe spores. The positions in which the latter are clearly present have been indicated by *S*. They were probably present in other loculi, but were welded together into an impenetrable mass, owing probably to the presence of some vestige of the spore mother cell, which, as in recent cycads, appears to have remained long enveloping the tetrad. In the specimen shown in figs. 11 and 12 the spores are free, and there is no welding together of the contents of the loculus. In text figs. 3 and 4 sclerotic plates are indicated by groups of hexagonal cells. Two vertical plates can be seen in text fig. 3 (*sp*), and where plates are incorporated with the wall of a loculus they are indicated by *s<sup>1</sup>p<sup>1</sup>*. Larger horizontal plates are also seen in text fig. 4 in the central region. Vascular bundles, their delicate ramifications and large nerve endings, are indicated by hatching. The wall of a loculus has apparently broken down, as shown in the center of both text figs. 3 and 4, and spores are found among the swollen fibers. In both diagrams there is strong suggestion of segmentation of loculi, as Professor BOWER kindly pointed out to me.

Although the distribution of the vascular strands is mainly peripheral, at least two may be found in the foci of the ellipse formed by a cross-section (text fig. 4, *vb<sub>1</sub>*, *vb<sub>2</sub>*), but the number cannot be

regarded as determined. The peripheral strands probably alternated with every two series of loculi, but owing to the obliquity of their course (fig. 10 and text-fig. 7) they are often difficult to distinguish. An interesting point in the structure of the sporange in detail is the absence of any evidence of the building up of the synangium by a fusion of sporangia. The whole body strongly suggests its origin from a single sporange which has shared in the same type of skeletal elements as the petiole on which it was borne.

The sporogenous regions were distributed fairly equally throughout the body, except that their disposition in the periphery probably was determined by the approximately dictyoxylon type of cortex. If the loculi appear to be of unequal size, this is due partly to the varying girth of the sporange, and partly to the plane of section through the loculus. Wherever a section occurs in the surface plane, as in the upper third of text fig. 3, the buttresses are seen to lie so obliquely that a transverse section necessarily cuts through the contained loculi at different angles, and explains the fact that a transverse section does not differ much in appearance from a longitudinal one, except in form.

GROUPING OF SPECIMENS.—The available specimens, roughly sixty in number, may be grouped in four classes:

CLASS I.—Specimens such as that occurring in CN.307.16-19 (figs. 11 and 12), where the vegetative tissue is subordinate in amount to the sporogenous tissue. Such specimens show septa, mesarch vascular strands, and only a few water storage elements. The sclerotic plates characteristic of *Heterangium* in such sporangia are well developed, both in the periphery and in connection with the deeper lying septa.

CLASS II.—Specimens such as those occurring in CN.411.30, 31 and CN.386.17, 18 (figs. 5, 10). These contain ripe, apparently normal spores and normally disposed loculi, but undoubtedly a larger proportion of vegetative tissue than those in class I (text figs. 3, 4). The following series also belong to this class: CN.386.7, 8; CN.395.5, 6, 18, 19; CN.396.4, 5.

CLASS III.—Specimens such as those occurring in CN.383.10-13 and CN.386.11, 12 (figs. 1-4, 8, 9). Although one of these is possibly an immature form showing carbonization of the spo-

rogenous tissue within the loculi, for example, CN.386.11, 12, it is not possible to be sure of the nature of the carbonized contents.

No recognizable spores occur in any of the specimens included in class III, and in several series of sections which exhibit the structure of the body from apex to base, such as that in CN.391.23-27, the loculi seem to be filled up by concentric series of blackened cells, and in some cases have a well defined nerve ending in the center (CN.391.26).<sup>2</sup>

The majority of the available specimens belong to class III, which may be taken to include also specimens such as that in CN.393.6A (fig. 13), in which vegetative development obtains to such an extent that the conclusion is obvious that they were abortive or almost completely so. These specimens are of value as demonstrating the extreme condition of the phenomenon, and render probable the suggestion that there was some degree of phyllody (approximation to pinna structure) even in those of class II. The sections showing vegetative development are sometimes slightly larger than those in the normal series CN.307.17-19.

### Significance of specimens in classes II and III

The explanation of the state of these sporangia, purely on the assumption of partial sterilization and maceration before impregnation with calcite, is not wholly satisfactory. In recent plants, when sporangia abort, the process affects the sporogenous tissue mainly, as in some specimens of *Angiopteris* sporangia, where the wall and apical crest (annulus) remain unaffected. A mucilage gland results in several familiar instances (7, 16). In the specimens under consideration, however, the loculi show no sign of a mucilaginous content, but, together with the septa, are represented by a considerable amount of tissue comparable with that in the vegetative pinnae of *Heterangium*, the parent plant.

KIDSTON and LANG (10) point out that the sporange in *Rhynia* and *Hornea* may be regarded as "corresponding to the tip of a branch of a thalloid sporophyte, inclosing sunken tetrasporangia."

<sup>2</sup> Tracheids possibly formed from degenerating sporogenous tissue of the ovule have been recorded by TREUB (17) in *Casuarina*, and by the writer (2) in *Castanea*, but it is an unusual phenomenon.

It is not an organ *sui generis*, but partakes of the same potentialities as other branches.

The widely accepted view that the Sphenopterid leaf is a meriphyte, and that the pinna corresponds with the cladodified primary branch axis, makes it easy to conceive of the microsporangium showing in some cases the same anatomical elements as the pinna. The Sphenopterid type of frond as recorded by ARBER (2) had already made its appearance in the Devonian, and *Heterangium Grievii* may well have retained some reminiscence of the earlier unspecialized condition from which we conceive the sporangium to be evolved. The curious specimens under discussion, which probably owe their preservation in a fossil form to their condition (as only two or three specimens of class I are so far recorded), are thus of considerable interest for the pinna-like character they exhibit. Nor is their more or less sterile condition without significance in any discussion as to the origin of the seed habit in *Heterangium*. Any comparable instability in the homosporous sporangia of the ancestor could well have been the beginning of a differentiation into megasporangia and microsporangia. A plant bearing vascular sporangia which retained but a few tetrads and relatively much surrounding vegetative tissue might well be regarded as on the high road to seed formation.

### Evidence of syngial origin of seed

It must have occurred to many morphologists that a seed was a transformed synangium, the nucellus representing the one persisting fertile loculus, and the inner integument the vestigial peripheral part. In 1904, the evidence then available for this theory of the syngial origin of the seed was discussed by the writer (4) in connection with the description of *Telangium Scottii*, a synangium very common in the Coal Measures of the Upper Carboniferous rocks of the north of England, and the first species of that genus to be described showing structure. There were at that time certain difficulties in the general acceptance of the theory, chiefly because the structure of *Telangium* was such that, while explaining the integument, the absence of any central loculus rendered the explanation of the nucellar or central fertile loculus of the seed difficult.

Thus, as the absolute parallel between seed and synangium could not then be demonstrated, there were critics who preferred to lay stress on the possibility of the seed having acquired its characteristic structure independently of its ancestral condition, rather than by a transformation of structures already present. The inner integument, as well as the outer or indusial envelope, was attributed to foliar upgrowths around the nucellus, which alone was regarded as the representative of the ancestral sporange. The views of such critics are summed up by OLIVER (13) in his account of *Physostoma elegans* in the following words:

The synangial theory, though no doubt tenable, presupposes in the ancestor the existence of the exceptional condition of a synangium, in which the peripheral members were ranged symmetrically around a central sporangium, and in which they persist as a sterilized envelope to form the seed coat.

Having at that time already secured several specimens which indicated the existence of a synangium with central loculi surrounded by peripheral ones, the writer took an early opportunity of collecting some more of the Pettycur deposits in which these interesting specimens occurred. By 1911, several hundred sections had been cut from two of the blocks collected the previous year. These blocks contained much *Heterangium Grievii* material, and yielded the large number of specimens now available of the new synangium. Owing to the care with which the stones were cut, many of the synangia, although scarcely 4 mm. in length and 2 mm. in width, are represented by series of three or four sections in the transverse plane or two in the longitudinal plane. The average thickness of the stone involved in the section cutting was 0.8 mm.

As already stated, the series of transverse sections CN.307.17-19, CN.343.10-13, and CN.412.30-31, although cut from different blocks, demonstrate clearly with many others that a synangium was present in these older rocks, associated with and showing the characteristic cortical structures of *Heterangium Grievii*, a synangium in which central loculi, as well as the more commonly occurring peripheral, occur. It is also interesting that even in the microsporangial apparatus an unusual amount of vegetative tissue obtained was also clearly shown for the first time. The publication of the details of the structure of *Sphaero-*

*stoma* in 1914 was to have been followed by the account of the microsporangium *Heterotheca*, but other things have claimed attention, and it has only been since November 1918 that the work has again been taken up. The investigation of a larger number of specimens has thrown new light on the structure of *Heterotheca*, especially on the character and differentiation of the non-sporogenous tissue. With the possible exception of *Crossotheca* (text fig. 8, II), it differs from all other described microsporangia, and approaches what must be assumed to be a synthetic type of seed and microsporangium. It is a succulent, sclerotic, vascular synangium, with central as well as peripheral loculi, and exhibits in its own tissues most of those found in the seed.

If we may have even in sporangia coexistent in the same species of plant a large amount of vegetative tissue, it is obvious that there is ground for assuming that in the early phases of evolution of the seed this would have been available as an envelope to the central fertile loculus, if the peripheral ceased to form sporogenous tissue.

A difficulty some have had in accepting the theory of the synangial origin of the seed has been expressed by the statement that "nothing useful has ever been produced by a sterilized sporangium." It is granted that abortive sporogenous tissue generally eventuates only in a mucilage cavity, as COULTER and LAND (7) and STARR (16) have shown in particular cases, but useful structures certainly can be formed by the elaboration of the vegetative tissue surrounding masses of sporogenous tissue, as has recently been demonstrated (6) in the megasporangium of *Mazocarpon*. It is not altogether sterilized potential sporogenous tissue of the peripheral loculi in *Heterotheca* which formed the inner integument of the ovule (canopy), but mainly an elaboration of the vegetative tissues which originally surrounded those masses of sporogenous tissue and finally supplanted them. For example, *Azolla* and all such leptosporangiate ferns were foredoomed to failure in the construction of a seed on these lines, as their peripheral sporangia had in all probability lost their vascular supply and their skeletal tissue before heterospory was evolved. The parallel to the seed habit which may be noted in *Azolla* is limited to the fact that the megasporangium is one-spored, and occupies a central position in the sorus.

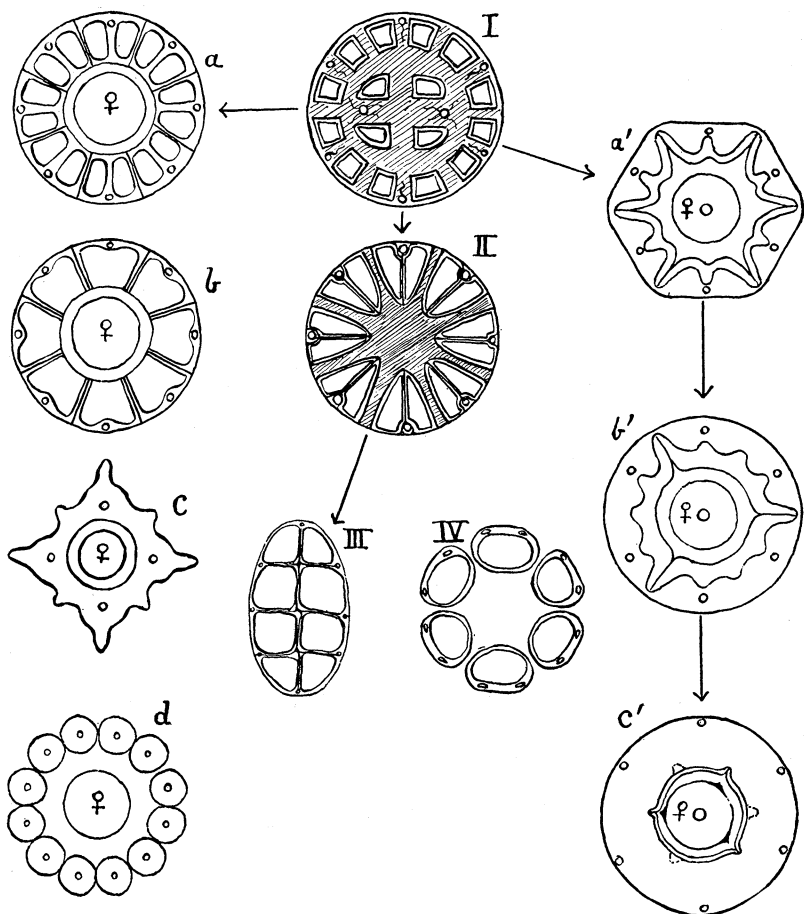


FIG. 8.—Diagrammatic transverse sections of various Pteridosperm ovules and pollen sacs to illustrate numerical relations they show to *Heterotheca* and one another: on left are *a*, *Sphaerostoma*; *b*, *Lagenostoma*; *c*, *Conostoma*; *d*, *Physostoma*; on right are *a'*, *Polylophospermum*; *b'*, *Trigonocarpus Parkinsoni*; *c'*, *T. Shorensis*; in center are *I*, *Heterotheca Grievii*; *II*, *Crossotheca Hoeninghausi*; *III*, *Telangium Scottii*; *IV*, *Codonothea caduca*. Vascular bundles indicated by small ring in each; arrows denote different phyletic lines; diagrams have been adapted from those of SCOTT and MASLEN, OLIVER, OLIVER and SALISBURY, SELLARDS, and three of writer's, references to which occur in text; relative size of bodies concerned has been neglected for convenience of comparison.

Lastly, a difficulty in the syngangial theory of the seed has often occurred to the writer, but she has not heard it expressed by others. It is that in the compartments of the canopy of *Lagenostoma* a vascular bundle occupied a central position instead of, as one might have expected, a position in the plane of the lateral walls. As will be seen in text fig. 8, this difficulty is completely removed by the structure of *Heterotheca* and *Sphaerostoma*. Each compartment in the canopy of *Lagenostoma* is equivalent to a pair of loculi, which, although completely merged in *Lagenostoma*, can still be faintly traced in *Sphaerostoma*.

We owe much to Professor OLIVER for the open expression of his views published in 1909. The conclusions he finally arrived at were opposed to those which seem necessarily drawn from our present knowledge. Both theories as to the origin of the seed were mere hypotheses in 1908. Unfortunately, the view that the canopy of *Lagenostoma* was the product of a cupular or indusial upgrowth, led to the further hypothesis that the *Physostoma* segmented integument was a relatively primitive form, and even contributed to a suggestion that *Physostoma* was perhaps the most archaic type of seed known, a suggestion wholly contrary to what is known of its geological history. In the light of recent work, these latter hypotheses necessarily fall together, and it is to be regretted that a recent writer (14) should have referred to them as facts. OLIVER merely claimed that certain conditions should be proved to exist "in the ancestor," but evidently the necessary conditions have persisted in *Heterangium*, so that they coexist with the formation of an ovule for the megasporangial apparatus. Thus a link is provided between an ovule and a microsporangium which is stronger than was demanded, and there can be no longer any question as to the seed of a Pteridosperm, a seed that may well have been the homologue of all Pteridosperm seeds, having been produced in the course of evolution as a transformation product of a syngangium. In this investigation we thus stand upon the threshold of the origin of at least one group of the Spermatophyta, and find more indications of it than were expected in the structure of a plant of the Lower Carboniferous.



The following is a more concise statement of the features of resemblance between *Heterotheca Grievii* and various ovules and microsyngangia regarded as homologous with it. For the better elucidation of the subject, text fig. 8 has been constructed showing the possible numerical relations, etc., between the various sporangia of the Pteridosperms. We will commence with a comparison of *Sphaerostoma* and *Heterotheca*.

*Heterotheca Grievii* resembles *Sphaerostoma ovale* in the following particulars. It is approximately of the same form and dimensions (length 3.5-4 mm., width averaging about 2 mm.). It has probably six peripherally placed bundles in the buttresses between every two loculi as seen in transverse section. Besides these, there are two in the foci of the ellipse of the cross-sectional area, making eight in all, as in *Sphaerostoma*, although in the latter all eight are peripheral. The bundles are accompanied by enlarged water storage elements, and branch as in *Sphaerostoma* (5), fig. 3a. There is a central fertile region in each. In *Heterotheca* there is a large amount of vegetative tissue in the region between the loculi, forming buttresses vertical to the surface similar to those of the canopy of *Sphaerostoma*.

The differences can be explained by progressions of well known type. Thus the overarching of the central region by the peripheral at the apex to form the micropyle and sinus may have been partly in relation to the necessity of harboring the pollen grains, and partly a direct result of the freer vegetative development of the periphery. The later segmentation of syngangia is a familiar phenomenon in Pteropsids, as may be seen by a comparison of *Angiopteris* and *Marattia*. The regular circumscissile dehiscence of the pollen chamber may be reminiscent of the time when there was a whorl of central loculi such as still exist in *Heterotheca*.

That there should be so few differences and so many resemblances between the microsporangium and the ovule of the same species, makes it impossible to homologize merely the nucellus with the microsporangium; as already stated, we must accept the syngangial origin of the ovule as a whole, and regard the nucellus as derived from the central part of the common ancestor of both *Heterotheca* and *Sphaerostoma*. That the two structures, borne by the same species,

should be homologous is undoubtedly the simplest explanation of their origin. They both separate from the frond, and in this respect differ from later forms, where, on the attainment of dry dehiscence in the microsporangium, the pollen escaped before the fall of the sporangium. The indusium or cupule which surrounds the ovule as long as it remains on the parent plant is one of the distinctive features of microsporangium and ovule, for there is no evidence of an indusium surrounding *Heterotheca*. This difference, however, is really confirmatory of the synangial origin of the inner integument, as such an origin does not involve a double indusial formation in a relatively primitive ovule. On grounds such as these, it may be assumed that in the particular case of *Heterangium Grievii* its microsporangia and ovules are homologous, both being transformation products of a common ancestor.

Those who accept this thesis will undoubtedly be prepared to accept it for all the other Lagenostomales, such as *Lagenostoma*, *Conostoma*, and *Physostoma*. A necessary corollary as respects *Physostoma* is that there has been a meristic variation in the periphery. The bundles are approximately, or we might say, potentially twice as numerous as in the periphery of such a sporangium as *Heterotheca*, and each dominates one radially symmetrical "tentacle" instead of a dual compartment as in *Spharostoma* (text fig. 8, *a, d*). Thus instead of regarding *Physostoma* as a *Lagenostoma* with unfused chambers (OLIVER 13), we should, in the light of *Heterotheca*, regard it as a *Lagenostoma* with a lobed canopy.

Turning from the Lagenostomales to the Trigonocarpeae, which are regarded as the ovules of some at least of the Neuropterideae, we may ask if they bear any internal evidence of origin from such a type of synangium as *Heterotheca*. They show obvious series in the structure of the integument, series which in some respects run parallel to those in the Lagenostomales. Excellent details of the integument will be found in SALISBURY'S (14) work on *Trigonocarpus Shorensis*. In the Trigonocarpeae the nucellus is free from the inner integument except in the plane of its basal attachment, through which runs a vascular bundle which eventually forms a tracheal envelope round the nucellus. Six other bundles enter the integument and travel in its periphery. *Polylophosper-*

*mum*, *Trigonocarpus Parkinsonii*, and *T. Shorensis* show an obvious series in the reduction of the compartmental character of their integument (text fig. 8,  $a^1$ ,  $b^1$ ,  $c^1$ ). In the two former the six bundles obviously alternate with compartments as in *Sphaerostoma* and *Heterotheca*, but in *T. Shorensis* all trace of the buttresses in the plane of the bundles has disappeared, as in *Lagenostoma*, and the bundles appear to occupy a central position.

The numerical relations of the bundles in *Heterotheca* and the Trigonocarpeae correspond, if we may assume in the latter a simple fusion of the two central bundles to supply the megasporange (nucellus), which in this series of seeds is free from the integument, and thus necessarily requires a central water supply. The tracheal mantle which becomes such a prominent organ in some of the Neuropterid seeds, for example, *Stephanospermum* (OLIVER 12), needs no explanation if the nucellus were derived from an ancestral sporange such as *Heterotheca*, with its large water storage equipment. Further, the succulent sarcotesta of the Trigonocarpeae is extraordinarily similar in structure to the succulent ground tissue of *Heterotheca*, so far as respects the macaroni-like tubules (text fig. 3). There is thus a considerable sum of evidence in support of the homology of the Pteridosperm seeds with a microsynangium such as *Heterotheca*.

Let us now turn to a consideration of the other microsporangia attributed with general assent to Pteridosperms. I shall only refer to *Crossotheca Hoeninghausi* (KIDSTON 9), *Telangium Scottii* (BENSON 4), and *Codonothea caduca* (SELLARDS 15). Of these, *Telangium Scottii* is the only one in which the details of the anatomy have been published, but the preservation of the other sporangia as incrustation fossils is exceptionally good, and it has been possible to learn much of their organization. *Crossotheca Hoeninghausi* shows eight peripheral pairs of loculi, each pair showing a single vascular bundle running up in its dividing wall. In the young condition the eight pairs are seen to be in close lateral approximation, so that they form a body resembling a stout undehisced *Telangium* with a wide base. In specimens recently provided by Mr. HEMINGWAY, there seems no reason to doubt that this younger condition (occurring nearer the tips of the fronds) represents an

undehisced condition of a synangium. In KIDSTON'S original description (9) the synangium was regarded as built up of eight discrete dual sporangia. In a transverse section kindly lent by Dr. KIDSTON, it was noted that the matrix within the ring of paired loculi was stained yellow, and this is suggestive of decayed ground tissue having been present originally where now only a boss of rock can be seen.

ZEILLER thought that the members of the whorl were sometimes coherent. If this be the true interpretation, *Crossotheca Hoeninghausi* occupies a position almost halfway between *Heterotheca* and *Telangium*. It resembles *Telangium* in the possession of a single peripheral series of loculi, in apical dehiscence, and its retention on the frond until the spores are shed. It resembles *Heterotheca* in the loculi being distributed one on either side of longitudinal discrete vascular bundles, in the possession of much sterile ground tissue, and in the number (sixteen) of its longitudinal loculi or loculi series. It differs from *Telangium Scottii* in the number of its loculi, and from *Heterotheca* in the absence of central loculi and in its apical dehiscence. I have no evidence as to the character of its ground tissue, but it is probable that it was non-cuticularized.

From these considerations I have included in text fig. 8, II an adaptation of KIDSTON'S fig. 9, indicating by hatching the supposed ground tissue which had perished in the incrustation. It would seem best to retain the name *Crossotheca*, as the body is sufficiently distinct from any species of *Telangium* to retain its separate form genus rank.

*Codonotheca caduca* is regarded by SELLARDS as probably a Neuropterid sporange. It is fairly safe to regard it as belonging to some Pteridosperm, and a reference to it may be useful. Like the *Trigonocarpus* seeds, it is provided with six peripheral bundles, but in this case each becomes duplicated. Like the canopy of *Physostoma*, the peripheral series have become lobed. There are no central loculi, which are so far only recorded for *Heterotheca*. *Telangium Scottii* has but half the number of loculi recorded for *Crossotheca*, a mutation probably having occurred comparable with that which gave rise to the reduced number of bundles of *Conostoma*, which shows but four (text fig. 8, c). The three series

shown in this figure, for example, the Lagenostomales (*a-d*), the Trigonocarpeae (*a<sup>+</sup>-c<sup>+</sup>*), and the microsporangia (I, II, III, IV) illustrate the fact that at least two lines of progression can be traced in Pteridosperm seeds, each with members suggesting an early descent from a sporange with paired loculi. These paired loculi occur in both *Heterotheca* and *Crossotheca*. A tendency to simplification is seen in all three groups, *Conostoma* among the Lagenostomales and *Telangium* among the microsporangia showing a halving of the number of parts. Again an example of lobing occurs in one seed of the Lagenostomales (*Physostoma*, text fig. 8, *d*), and in one type of microsporangium (*Codonothea*, text fig. 8, IV).

### Summary and conclusions

1. Among the remains of *Heterangium Grievii* (vegetative organs and seed) in the calcified deposits of plants occurring at Pettycur, Fifeshire, have been found large numbers of a new type of microsporangium for which the form genus *Heterotheca* has been constructed.
2. Its mechanical structure is similar to that of the petioles of *Heterangium*, and, although so far found detached, it is attributed to *Heterangium* on the same grounds as are the vegetative organs, that is, the presence of vertical and horizontal sclerotic plates.
3. Its spore bearing tissue is distributed in sixteen series of loculi, of which twelve are peripheral and four central. The vascular bundles are similar to those of the seed, and near the apex each is nearly surrounded by a pair of loculi as in the canopy of the seed.
4. The structure throughout is strongly confirmatory of the homology of the seed and synangium, and is regarded as supplying ample proof of the synangial origin of the seed.
5. In this investigation we seem to stand upon the threshold of the origin of at least one group of the Spermatophyta, and the conclusions reached cannot fail to have their influence on the study of other groups.

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## EXPLANATION OF PLATES IV AND V

The following abbreviations are used in the illustrations: *b*, buttress or interstitial tissue between peripheral loculi; *e*, epidermis; *g*, gap in stone section; *gt*, ground tissue; *l*, loculus; *cl*, central loculus, *ne*, nerve ending; *s*, spores; *sp*, sclerotic plate; *sp<sup>l</sup>*, plate attached to loculus wall; *vsp*, vertical sclerotic plate; *vb*, vascular bundle.

## PLATE IV

FIGS. 1, 2.—Two successive cross-sections of immature synangium; epidermis is preserved, and in center of body occur small sclerotic plates; no central loculi can be distinguished, and content of peripherous ones is amorphous; matrix has been left around fig. 1 (CN. 386. 11, 12);  $\times 33$  diameters.

FIGS. 3, 4.—Two successive cross-sections of synangium nearer base; central loculi well shown (CN. 383. 12, 13);  $\times 29$  diameters.

FIG. 5.—Transverse section of mature specimen, showing many of loculi with ripe spores, some of which, owing probably to solution of loculus wall, lie free in ground tissue; rough diagram of this section given in text fig. 4 (CN.411.31);  $\times 37$  diameters.

FIG. 6.—High power photograph of central ground tissue of obliquely longitudinal section, showing highly organized nerve ending (*ne*), various horizontal sclerotic plates, and succulent ground tissue like that of sarcotesta of *Trigonocarpeae*; in original, striated elements of transfusion tissue can be seen above nerve ending (CN.304.2);  $\times 100$  diameters.

FIG. 7.—Transverse section through upper part of synangium, showing central loculi and position of nerve ending (CN.411.12);  $\times 18$  diameters.

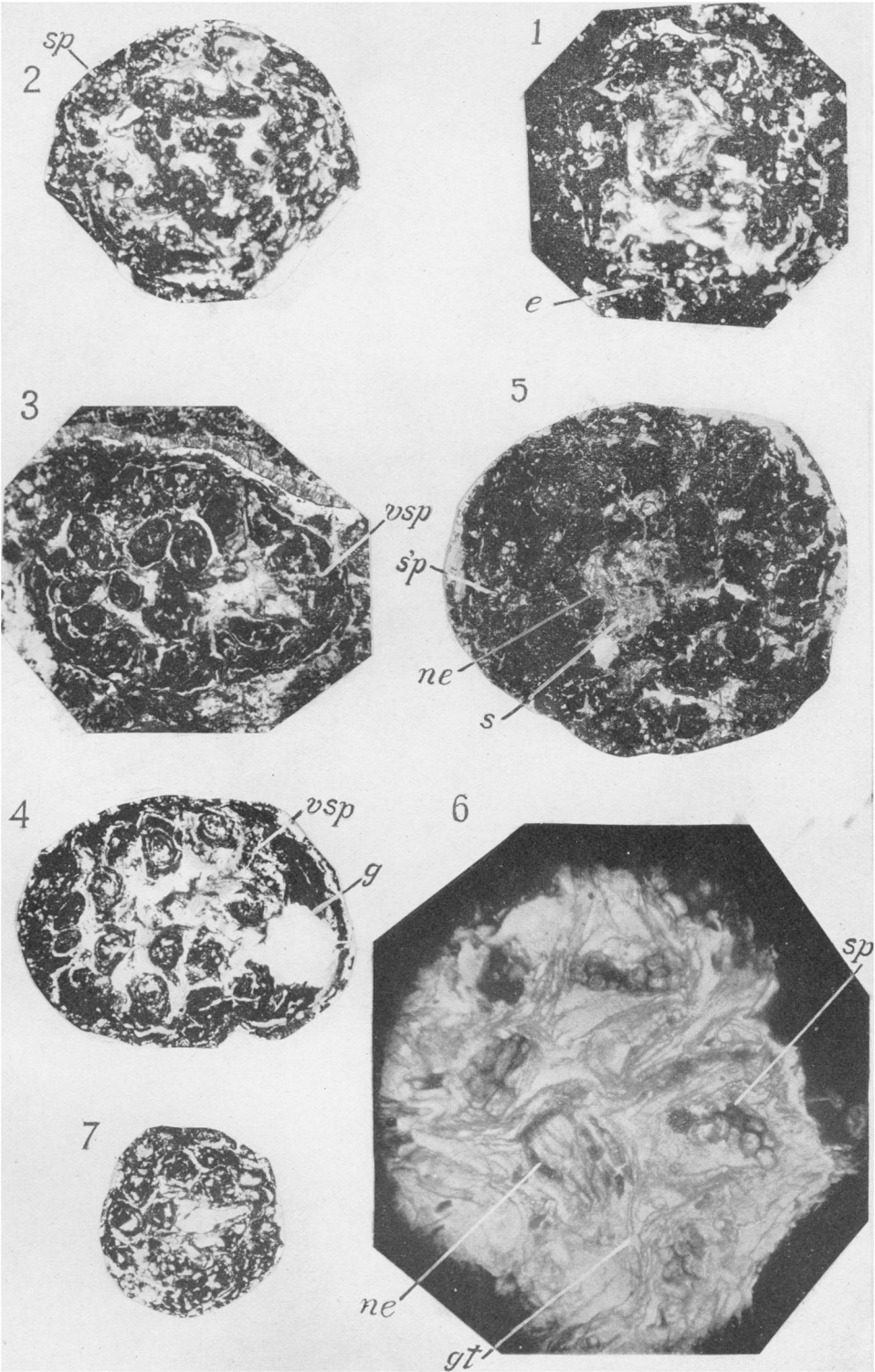
#### PLATE V

FIGS. 8, 9.—Two sections across another synangium, showing position of loculi in spite of some degree of maceration and subsequent shrinkage; in fig. 8 plane is nearer apex; surface is seen abutting on other tissues in matrix; in none of the four sections of this series are spores to be detected; fig. 8 (CN.391.23),  $\times 25$  diameters; fig. 9 (CN.391.24),  $\times 40$  diameters.

FIG. 10.—Nearly peripheral tangential section, showing in original the transversely oriented series of loculi, of which majority show tetrads of spores; cf. text fig. 3, constructed from two successive longitudinal sections; it is given to show transversely running strand (*vb*), for which reason the rest is slightly over exposed (CN.386.17);  $\times 42$  diameters.

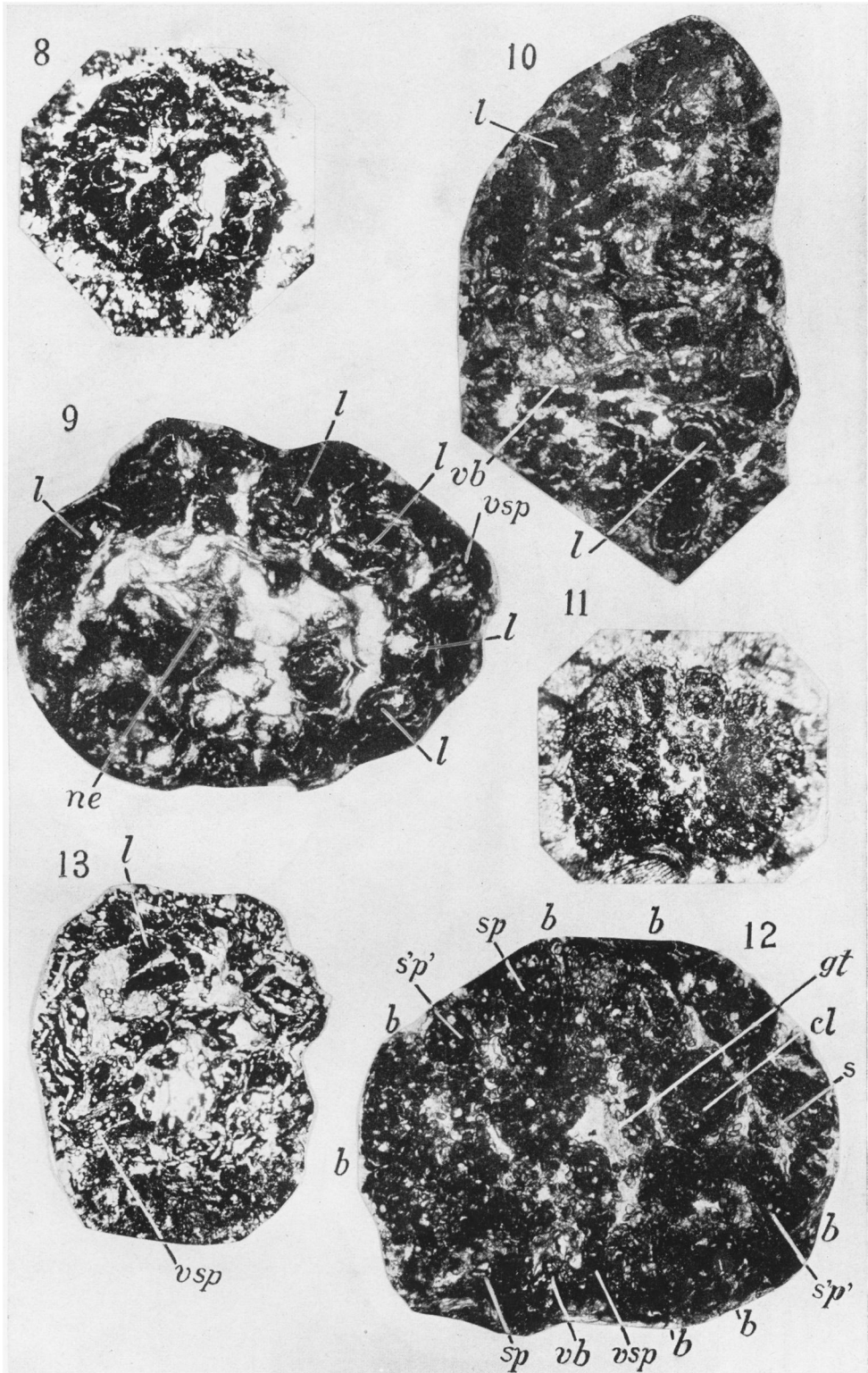
FIGS. 11, 12.—Two successive transverse sections of class I synangium, in which spores are free from one another and all loculi are full of them; synangium had undergone some degree of maceration, as shown by sclerotic plates (*sp*), cells of which show partial solution of middle lamella; key provided for fig. 12 in text fig. 6, to indicate position of sclerotic plates, loculi, etc., which are clearer in the fossil, although many of the walls have given way; fig. 11 (CN.307.17),  $\times 27$  diameters; fig. 12 (CN.307.18),  $\times 50$  diameters.

FIG. 13.—Transverse section clearly showing vertical sclerotic plates (*vsp*); most of loculi have perished, but one is indicated (*l*); several others are easily detected in the slide (CN.393.64);  $\times 32$  diameters.



BENSON on HETEROTHECA





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